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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS[1]

CHARLES C. ADAMS

PROFESSOR OF FOREST ZOOLOGY, THE NEW YORK STATE COLLEGE OF FORESTRY AT SYRACUSE UNIVERSITY

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I. INTRODUCTION

MY subject, "Migration as a Factor in Evolution," is, in other words, the function or rôle of migration in evo-

[1] This paper was prepared, by invitation, for the symposium on the Factors of Evolution, at the Pittsburgh meeting of the American Society of Naturalists and an abstract of this paper, entitled "Migration as a Factor in Evolution," was read January 1, 1918. Dr. G. H. Shull, president of the society, has kindly consented to its publication in advance of the volume which is to contain all the papers of the symposium.

lution.[2] In view of the recent concentration of interest on heredity, my subject has the flavor of an old-fashioned one, which calls back to the days when Darwin and Wallace were living, and when Wallace's "Island Life" was frequently read with enthusiasm, and when there was possibly a more general belief that natural selection was one of the large factors in evolution. But progress has not been limited to the studies of heredity, for with the rapid rise of certain phases of general physiology, animal behavior and animal ecology, a newer orientation is now possible with regard to the migration of animals by both the active and passive methods. For our knowledge of animal responses, as well as the influence of the vegetational and physical environment, have made considerable progress, and we now probably see more clearly than ever before the intimate relation existing between the animals and the conditions which influence their migrations. The present occasion has thus furnished an opportunity to make a preliminary reorganization of the accumulated materials from a somewhat different standpoint than was formerly current in discussing migration. And although some of these ideas are widespread and even commonplace in certain limited fields, yet they are not yet in as general use as is desirable, and they are in urgent need of extended application and critical study.

In the following discussion of migration as an evolutionary factor, I wish to emphasize two points in particular. One is the discussion of the process of analysis and the other is to suggest some methods of applying this method to the problem of migration. It may seem aside from the main thesis to give this emphasis to the process method of evolution, but after striving several years for the conscious application of this method in an allied field (Adams '13, '15), and seeing its beneficial results there,

[2] By evolution, I mean to use the term in the broadest possible sense—to include all changes within the organism and its necessary environmental implications, and not as limited to the "species problem." This term must be as thoroughgoing as metabolism in physiology, or as metamorphism as applied to rocks by Van Hise, "any change in the constitution of any kind of rock."

and furthermore, not having seen this formulated and applied to evolution as here presented, I feel that the importance of the subject merits this treatment.

Special attention is called to the fact that this discussion is not intended as a complete, scientific explanation of migrational facts, but as the presentation of a point of view, or working hypothesis, which it is believed will aid in explaining many well-known facts and relations, and will aid in the discovery of new ones. An effort has been made to frame this hypothesis in such a manner as not to prejudice the problems investigated, or to interfere seriously with the various constructive schools of investigation, although I am well aware that this hypothesis, like all others, is built upon certain assumptions.

During the preparation of this paper (which amplifies certain ideas which I have previously outlined) I was much impressed by finding so much confirmatory evidence of the general validity of the dynamic standpoint, in fields relatively remote from migration. The independent growth of such conceptions in diverse fields is indicative that many subjects are independently reaching a certain common stage of development and that spontaneously such ideas are becoming independent organizing centers of activity. By interaction and regulation among these ideas, new higher systems of unity and correlation are developing, which are producing important effects in zoology as well as in other sciences. The slowness seen in the application of dynamic ideas to biology is perhaps rather natural as is evident when we recall the fact that even in the simpler physical sciences we have as yet no complete dynamical theory or system, although much progress has been made, not, however, toward a complete system, but toward that dynamic equilibrium which characterizes a growing subject.

II. The Process Method of Animal Responses

1. *Introduction*

The fundamental assumption upon which this discussion is founded is that the animal should be looked upon

as an entity or agent whose system of activity or responses to internal and external influences are its most fundamental characteristic. The activity of the animal, as an agent, is its *process* of change or its process of activity. Broadly speaking, this is a study of influences, of response or behavior, a study of what animals do and how they do it. Throughout it is the *dynamic* aspect of the animal; the pressure it exerts upon the environment; and the pressure exerted by the environment on it, that is of greatest importance. I see no reason why these assumptions can not be of universal application, and why they can not be accepted in all investigation. This view appears to be so well established that no detailed evidence and discussion of it seems necessary at this time. The animal agent itself is not a fixed thing, but one which runs through a cycle; it originates, develops and disintegrates and is thus in its maintenance subject to all the ebb and flow of other processes, and has similar dynamic relations. There is thus valid reason for assuming a thoroughgoing process or dynamic program for dealing with all animal problems. The same is equally true of all plants which form a part of the animal environment, and the physical environment lends itself, in fact, easily leads, in such a treatment, and fits into this scheme harmoniously, and makes it possible to give not only a uniform treatment to all phases of animal relations, but enables the student of animals to make a perfect contact with all the allied sciences, and to draw from each one all possible support, with the least possible friction and interference.

2. *Dynamic Principles*

(*a*) *Activity of Agent.*—In discussing animal problems from the process standpoint there are several conceptions which are fundamental. These ideas can be illustrated in simple form by an example from physical science. Running water is a substance combined with energy (gravitation) which exerts stress or pressure, which it expends upon other substances, and it is therefore an agent. An agent thus exerting stress and expend-

ing gravitational energy upon other substances is in the process of activity. Thus, running water, by the general process of erosion, including the subsidiary processes of weathering and transportation, wears down the land and results in the formation of many features such as brooks, creeks, plains, deltas, and a variety of other physiographic products. An organism is also an agent which expends physical and chemical energy, producing stress and exerting pressure and expending energy on other substances, exhibits its process of response or its *process of behavior*. An animal, by the process of predation runs down another animal and devours it, by its *process* of digestion dissolves it, and by the process of assimilation makes muscle, bone, feathers or fur out of it, and these are all products of its activity. The process of response is here strictly comparable to the process of erosion of running water, and their products are similarly comparable. The general process is generic and includes many species and varieties of subsidiary processes, *ad infinitum*. As Keyes ('98) has well said, "Processes are merely operative. If coupled with products at all . . . they must be regarded as formative or constructive. The product's destruction, its loss of identity, is wholly immaterial. The action of agencies is merely to produce constant change." It is, therefore, to the process of living, to the process of evolution, rather than to its products such as species, varieties, etc., which are of fundamental importance. For this reason the products must be subordinated to the agencies and processes, because the laws of change are in reality the object sought.

The physiographer is not content to rest with the idea that the agent, as, for example, running water, is the finished product of his analysis, for he also applies the same methods of investigation to the agent itself, in order to know its method of origin, the *process* by which it originates in the stream, whether indirectly from a spring, or directly from the clouds. Thus the same methods which the physiographer uses in studying the activity of the agent, he again uses to explain the origin or derivation

of the agent iself. The investigator of animals follows the same plan. He likewise uses the same kind of methods in the investigation of the processes of functional and structural development, not only as applied to the actions of the agent, but to its origin as well, and thus again we are justified in concluding that the process method is of universal application.

(*b*) *Cycle of Activity.*—The activity of agents is always accompanied by the expenditure of energy. This expenditure does not take place at a uniform rate, there is a pulsation, an ebb and flow, a rising and a falling. Periods of activity are followed by periods of repose and a rhythm is seen which can often be resolved into cycles. The importance of determining such cycles has been well expressed by Lockyer[3] as follows:

> Surely in meteorology, as in astronomy, the thing to hunt down is a cycle, and if that is not to be found in the temperate zone, then go to the frigid zones, or the torrid zones and look for it, and if found, then above all things, and in whatever manner, lay hold of, study it, record it, and see what it means. If there is no cycle, then despair for a time if you will, but yet plant firmly your science on a physical basis . . . and having gotten such a basis as this, wait for results.

There are innumerable cycles in the responses of animals, and of these the life-history cycle is perhaps the most generally recognized; but activity and response, hunger and satiety, stimulation and response, are other familiar expressions of these conditions. During these cycles of change the relative amount of energy set free varies greatly, in other words, its *dynamic status* changes. As expressed elsewhere, I have stated ('15, p. 10):

> When a great amount of energy is being set free, when an animal is exerting much influence, we may look upon it as producing pressure or strain. A condition of stress is not a permanent one, because the pressure tends to cause such changes as will equalize or relieve this condition. This is considered as the process of adjustment to strain, and is Bancroft's law ('11). An animal in an unfavorable condition is stimulated, its normal activities are interfered with, and a physiological condition of stress is produced which lasts until, by repeated responses or

[3] "Solar Physics," 1874, pp. 424–425.

"trials," the animal escapes stimulation or succumbs and a relative equilibrium is established. An area becomes overpopulated and consequently there may be established a condition of stress which results in an adjustment by a reduction (through many causes) in the excess of population and a restoration of the normal, or a condition of relative equilibrium. From these examples it may be seen that the *dynamic status* means the condition of a unit or system with regard to its degree of relative equilibrium. The cycle of change may be considered to begin at any point. I have taken as the initial stage of the cycle the condition of *stress* and *pressure* and have indicated how this condition tends to change in response to pressure, bringing about the *process* of adjustment to strain, and leading to the *condition* of adjustment to strain, or that of relative equilibrium. The activity of the agent produces the condition of stress, the process of adjustment to the strain follows, and this leads to the product—the establishment of the condition of adjustment or of relative equilibrium.

These ideas can be well applied to the life cycle, as is indicated from the following statement by Sedgwick ('10, p. 177), who says:

> The life-cycle, of which the embryonic and larval periods are a part, consists of the orderly interaction between the organism and its environment. The action of environment produces certain morphological changes in its organism. These changes enable the organism to come into relation with new external forces, to move into what is practically a new environment, which in its turn produces further structural changes in the organism. These in turn enable, indeed necessitate, the organism to move again into a new environment, and so the process continues until the structural changes are of such a nature that the organism is unable to adapt itself to the environment in which it finds itself. The essential condition of success in this process is that the organism should always shift into the environment to which the new structure is suited—any failure in this leading to impairment of the organism. In most cases the shifting of the environment is a very gradual process (whether consisting in the very slight and gradual alteration in the relation of the embryo as a whole to the egg-shell or uterine wall, or in the relations of its parts to each other, or in the successive phases of adult life), and the morphological changes in connection with each step of it are but slight. But in some cases jumps are made such as we find in the phenomena known as hatching, birth, and metamorphosis. . . . And with this property of reacting to the environment goes the further property of undergoing a change which alters the relation of the organism to the old environment and places it in a new environment.

It is seldom indeed that one finds ontogeny so clearly expressed in terms of an active agent which is under-

going a cycle of changes—both in structure and function—and is being stimulated, responding, behaving, and even migrating into new environments, in response to internal and external stimulation. This is indicative of the dawn of a new era in the study of ontology (cf. Thompson, '17). As Bancroft ('11, p. 178) suggested, Sedgwick ('10, p. 177) saw clearly for the moment, as it were, but not in practice and concretely, the dynamic conception of individual development, although it is very evident that he saw the unity or continuity of the ontogenetic cycle. However, it has remained for Child ('15, '15*a*, '15*b*) who, apparently adapting largely the dynamic conceptions of the plant and animal ecologists, and to a lesser degree those of the physiologists, has now given expression, in a clear and concrete manner, to the dynamic ideas in individual developmental responses, and special attention is called to his important work.

That the life cycle varies in its degree of susceptibility to environmental influence has been pointed out by Vernon ('99, p. 199), DeVries (1900), Bancroft ('11, p. 175), and others (Woods, '10; Pike and Scott, '15; Pike, '17). Vernon's law is expressed ('03, p. 199) as follows: "In fact, it would seem to be a law of general application that *the permanent effect of environment on the growth of a developing organism diminishes rapidly and regularly from the time of impregnation onwards.*" Bancroft was the first to see that his law included Vernon's. He said ('11, p. 175):

> We know that, as we get older, our tendency to resist change increases; our habits of body and mind become more fixed.[4] We should therefore be tempted to conclude that the resistance to change increases as the organism becomes mature and that a given stimulus would probably have the most effect if applied at or before the earliest stages of development.

[4] In this connection it is interesting to recall the influence which this law may have upon scientific research. Once Clerk-Maxwell wrote to Herbert Spencer about some point in his "First Principles" as follows: "It is seldom that any man who tries to form a system can prevent the system from forming around him; and closing him in before he is forty. Hence the wisdom of putting in some ingredient to prevent crystallization and keep the system in a colloidal condition." (Footnote by C. C. A.)

He then quotes Vernon and continues:

> If the pressure on a liquid is made less than the vapor pressure for that liquid at that temperature, some of the liquid vaporizes, the temperature falls, and the liquid may be said to adapt itself to the new conditions. What would happen if the liquid were not adaptable? The easiest way to obtain non-adaptable liquid is to place a Bunsen burner under it. The temperature rises until the boiling point is reached. The liquid then ceases to be adaptable. It volatilizes, it disappears, it becomes extinct so far as that particular region or flask is concerned. If a species can not adapt itself to changed climate or other conditions, it does not volatilize; but it disappears, it becomes extinct. It may be a new point of view to consider the extinction of the mastodon as analogous to the distillation of water; but the two cases are really parallel, except in time.

These facts are of the greatest importance because they indicate the *critical stage or condition* at which, in the migration of animals into new localities and conditions, organisms are most likely to be modified, and thus influence their evolution. This furnishes a new reason for stressing the importance of the breeding conditions and habitat in ecology.

An exception to Vernon's law is to be seen in the case of the Protozoans (and probably to other kinds of non-sexual reproduction), as is indicated by Jennings ('12, '13) and Woodruff's investigations, which show that in a proper environment the inertia of the life cycle tends to continue on indefinitely and does not run down. Jennings ('12, pp. 573–574) shows that conjugation in Protozoa and sexual reproduction in the metazoa cause diverse and new combinations of characters. In other words, this means that the processes of conjugation (favored by adverse conditions) and sexual reproduction, tends to break up the stability and crystallization into which the ontogenetic system tends to develop, and tends to restore, as it were, flexibility and a colloidal state to the race. This changes the system so as to minimize the interference with its processes. In the metazoan the number of systems is so large, that in spite of its chemical integration and regulation, interference with one or more of

them, possibly the "slowest," limits action and causes death. As indicated later, according to the phase rule the greater the number of "phases" interacting the lesser the number of possibilities of change. This is not a condition limited to organisms, but is a general law. It is perhaps in some sense as this that we can concede "differentiation" as a cause of death.

The animal as an agent, or individual, behaves according to its own system, to the extent that it is an independent unit, and these activities are cyclical. All systems tend to perpetuate themselves. Bancroft's law for all systems is that: "The broadest definition of it is that a system tends to change so as to minimize an external disturbance." In other words this is a perpetuating tendency, a method of assimilation, of which reproduction may be considered but a special phase; it is not solely a peculiarity of organisms, as is often stated, but of *all systems*. Sedgwick ('10, p. 177) has said: "It is a property of living matter to react in a remarkable way to external forces without undergoing destruction. . . . This property of reacting to the environment without undergoing destruction is, as has been stated, a fundamental property of organisms." In these features the animal acts only as other systems tend; as a catalyzer, it hastens changes and maintains itself. The activity of the animal, its centrifugal stress, causes it to collide with its environment, while, on the other hand, there is the environmental bombardment, both of which, within certain limits, tend to interfere or destroy the animal. On the other hand, the tendency of the system is to "minimize disturbance," to change within, to minimize, to "retreat" from interference (absolutely or relatively), and in this manner to a large degree, the system is perpetuated. To be sure, many individuals perish, but the system of the species continues. The rate of change of the system can be modified only as fast as its *slowest member* can change, and on this account many individual systems are destroyed.

In addition to influences which "interfere" with sys-

tems, as expressed by Bancroft, there are those which *reinforce* or accelerate (tend to continue or hasten activity) and do not change its character, but only the intensity of the response (temperature, enzymes, repetition, etc.). By this method also systems tend to be perpetuated, and organisms in "favorable" (non-interfering) conditions, tend to continue their normal activities.[5] This law appears to be a corollary of Bancroft's law which is concerned with interference or retardation. Thus when a system is *reinforced,* rather than disturbed, the system continues onward in its normal cycle without interference, and may even be accelerated in its activities. This is a condition which may maintain a relative equilibrium, or increase stress. The intensity of interference, or reinforcement, and its repetition, hastens or retards the rate of change of a system. We thus have the qualitative and quantitative relations applying to the law of reinforcement or acceleration of the equilibrium, and Bancroft's law of interference with its development.

Even relatively fixed and automatic responses of behavior may be looked upon much as the relatively stable structural characters, so that every sort of behavior, even to the process of higher learning, shows this regulatory influence which tends to change in such a manner as to eliminate all disturbance with its systems, even to the inconsistencies of our ideals.

Thorndike ('11, p. 244) in summarizing the laws of "acquired behavior or learning" formulates two laws. The first is essentially a statement of Bancroft's law of response to interference (discomfort or satisfaction), and the second (exercise or repetition), is that of reinforcement. This means that the kind and intensity of stimulation, and its repetition are the laws of establishing associations, or of changing the system, and that *intensity and repetition* act as the catalyzers which influence the speed of modification of the system; at bottom it therefore appears we have qualitative and a quantitative

[5] Cf. Jennings, '06, p. 295, "positive reactions."

expression of them. Limiting factors, because of their intensity and repetition, tend to change the animal system so as to minimize the external disturbance, or the animal system tends to change in such a manner as to minimize external disturbance, at a speed determined by the intensity and repetition of the disturbance. The so-called "trial and error," or, better, trial method of behavior, is also an independent formulation of Bancroft's law. It seems probable that the modifiability of behavior, and even *all methods of animal regulation, are expressions of these laws of interaction.*

The "balance of nature" is a culminating phase of the cycle of adjustment to strain. As expressed elsewhere, I have said (Adams, '15, p. 14): "When a balanced condition, or relative equilibrium, in nature is referred to, we must not assume that all balances are alike, for some are disturbed with little effort and others are exceedingly difficult to change. This distinction is an important one. Once the balance is disturbed, the process of readjustment begins. This is a phase in the balancing of a complex of forces. Just what stages this process will pass through will depend, to an important degree, upon the extent of the disturbance. Slight disturbances are taking place all the time and grade imperceptibly into the normal process of maintenance, as when a tree dies in the forest and its neighbors or suppressed trees expand and take possession of the vacancy thus formed. Disturbances of a greater degree, on the other hand, may only be adjusted by a long cumulative process. This change can progress no faster than the rate at which its slowest member can advance. Thus a forest association of animals may be destroyed by a fire so severe that all the litter and humus of the forest floor is burned. The animals which live in the moist humic layer as a habitat, such as many land snails, diplopods, and certain insects, can not maintain themselves upon a mineral soil, rock or clay. As such a forest area becomes reforested, these animals can only find the optimum conditions when the slow proc-

ess of humus formation reaches a certain degree of cumulative development. Under such circumstances this later stage must be preceded by antecedent processes, and the restoration of the balance is long delayed. Some adjustments take place so quickly that little can be learned of the stages through which they pass. There are, however, many slow processes which afford an abundance of time for study; in fact some are too slow to study during a life time. The processes which are moderately slow are often particularly illuminating because all stages are frequently so well preserved that comparison is a very useful method of study; the slowness of a process has a certain resolving power, as it were, recalling the influence of a prism upon a beam of white light, which reveals many characteristics obscure to direct vision. A study of the processes of adjustment among animals is a study of an important phase of the problem of maintenance. The continued process of response will, if circumstances permit, lead to a condition of relative adjustment, or balancing among all the factors in operation.'' The determination of the dynamic status and its application to cycles is seen to be a method or criterion which may be used for the determination of cycles of activity, and the repetition of these determinations will indicate the direction of movement of a process, and thus serve as a guide in the determination of its rate of change.

(*c*) *Limiting Factors.*—Animals live in a real world, they are dependent upon an environment and they can not be understood independently of it. They do not live, as it were, in a vacuum. As Brooks ('02, p. 485) has said: ''No physiologist who studies the waste and repair of living bodies, no naturalist who knows living beings in their homes, no embryologist who studies the influence of external conditions upon development, can, for an instant, admit that living beings are self-sufficient or self-sustaining, or that their being is in themselves; for the line we draw, for our study, between living beings and the external world is not one we find in nature, but one

that we make for our own purposes." We have seen that the essence of the animal is its activity. Its life is a continuous collision with the environment and a bombardment by the environment, with changes which tend to relieve the disturbances. This is particularly true of free-living animals, and is indirectly so, even of sedentary and sessile kinds. This radiating activity of the animal, and the direct convergent influence of the environment on the animal, is the basis for the friction and interaction which exists between the organism and the environment. There are, therefore, definite zones of influence and stimulation about the normal or attuned environment of the animal, and with departure from these conditions locally and geographically there are certain definite results (Adams, '04, p. 211):

> The new vital conditions are a cause of stimulation and with further departure (beyond a certain limit) it leads to increased stimulation or to unfavorable conditions. This results in retarded growth, development, and reproduction of the organism as a whole. Thus the end results of extreme departure from the optimum in either direction are similar.

(Adams, '15, pp. 8–9):

> Thus departure from the optimum toward an increase or a decrease, are departures from the most favorable, conditions toward less favorable conditions and hence toward limiting conditions. . . . In nature we look upon the optimum as that complex of habitat factors which is most favorable, and departure in any direction from this optimum intensity is in the direction of a less favorable degree of intensity, or into unfavorable conditions. From this standpoint *any unfavorable condition is a limiting factor* and may retard, hasten, or prevent vital and ecological activities.

(Adams, '13, p. 98):

> The similar results of extremes of high and low . . . temperatures, aridity, and the lack of oxygen may be cited as examples. Such effects have an important bearing upon the subject of physical and chemical *limiting factors* which influence individuals. [Cf. Shelford, '11, pp. 598–599.]

I would now modify my preceding quotations so as to definitely discard the old idea of the optimum,[6] in harmony

[6] This word has a general utility, but its technical value, like that of the "normal," both long considered peculiar to organic response, appears to be limited.

with the suggestions of Blackman and Smith ('11) who show that certain physiological processes are better explained as the "result of interacting limiting factors than by the conception of the optima." This principle is an extension of the law of the minimum and is formulated by them as follows (p. 411):

> The identification of the particular limiting factor in any definite case is carried out by applying experimentally the following general principles. *When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function* . . . (p. 397). When several factors are possibly controlling a function, a small increase or decrease of the factor that is limiting, and of that factor only, will bring about an alternation of the magnitude of the functional activity.

Probably this formulation should be broader, and be made to include not only a single factor, but all unfavorable or limiting factors, as I have indicated above, and as both Livingston ('17, p. 8) and as Hooker ('17, p. 201) suggest.

Recent additional physiological evidence of the concentric zonation (gradation) of the limiting factors of temperature and humidity have been made by Pierce ('16). He accepts the older idea of the optimum and thus certain of his results on zonation harmonize with my statement of 1904. He shows that for the cotton boll weevil there is a vertical temperature gradient which influences the metabolism, growth and other activities, and that for a given temperature there is a corresponding horizontal humidity gradient which forms concentric zones of less favorable conditions. These extend from the optimum, through dormancy, on to death. It seems likely, however, that the idea of "interacting limiting factors" explains his facts better than that of the optimum.

The idea of limiting factors in experimental work is now building up a laboratory idea of environmental complexity, even under controlled conditions, which corresponds closely with what the field ecologists have called

an environmental complex. This is a healthy sign as it will greatly assist in the correlation of field and laboratory studies. Recently Livingston ('17, p. 8) has said:

I wish now simply to emphasize the point that we can no longer speak of a single condition as being a cause of an observed effect. The next generation of physiologists will have to learn to handle more than a single variable and to deal with *complexes* of conditions.[7]

This recalls John Stuart Mill's statement that:

It is seldom, if ever, between a consequent and a single antecedent that this invariable sequence subsists. It is usually between a consequent and the sum of several antecedents; the concurrence of all of them being requisite to produce, that is, to be certain of being followed by the consequent. In such cases it is very common to single out one only of the antecedents under the denomination of cause, calling the others merely Conditions. . . . The real cause is the whole of these antecedents; and we have, philosophically speaking, no right to give the name of cause to one of them, exclusively of the others. . . . All the conditions are equally indispensable to the production of the consequent; and the statement of the cause is incomplete unless in some shape or other we introduce them all.

When Hooker ('17, p. 201) states that, "It is necessary to get away from the custom of discussing causes, however difficult this may be. The idea of causation invariably indicates *incomplete analysis*," he does not express the full significance of Livingston's remark. We have not yet outgrown Mill's statement.

In addition to its application to the individual animal, Bancroft's law applies with equal force to the dynamic tendencies of plant and animal associations. The dominance of a climax society shows that (Adams, '08, p. 125):

Such dominance, in general, implies extensive range, relative abundance, and ability to indefinitely succeed or perpetuate itself under given conditions. . . . The primary environmental conditions tend to encroach upon all others. The local conditions thus tend to become transformed in the direction of the dominant environment and to be appropriated by it. The associations . . . are thus given a definite dynamic trend. . . . Minor environments tend to become encroached upon by the dominant regional influences and ultimately to become extinct. The succession of socie-

[7] Cf. Blackman, '05, p. 293, on the limitations of control experiments. C. C. A.

ties of local habitats is a declining one, while that of the geographic or climax habitat is an increasing and ascending one. . . . That the dominant geographic conditions tend to override local influences seems very fairly established because diverse local original conditions are transformed into the climax or dominant type.

To students of human economics (for except ecologists we seem to have almost no students of general economics, including wild animals and plants) Bancroft's law should be a revelation. The interference or friction seen in economics (Conant, '08) should be included under Bancroft's law. That these laws apply to human social conditions as well can easily be tested by any one who will venture to "interfere" with any system of social machinery, whether it be of the family, fashion, church, state or a political party, for very soon the pressure or stress exerted by the "system" will make itself evident, by the processes of coercion, persuasion, ridicule, proselyting, threat, ostracism, or by a final crushing effort; for interference with a dominant system whether it is large or small has but one tendency. Years ago Bagehot ('73, p. 97) clearly recognized what appears to be essentially the laws mentioned above, and applied them with great skill to the development of political history, under the names of "persecution" and "imitation." Persecution corresponding to interference and imitation to acceleration. Hooker ('17, p. 208) not recognizing Bancroft's law, suggests what he calls the "principle of integration" to cover the interaction of the systems which he recognizes. He says: "These systems are invariably overcoming the effects of limiting factors."

(*d*) *Interaction of Systems.*—The next higher category, above the animal system, is the *interaction of the systems,* and their principles of complex action. To be sure, the animal system can not be divorced from its environment, so that several important features of this interrelation have already been discussed briefly. In dealing with the organism and the environment these two gross systems are perhaps the most clearly recognized in biology. The

environmental complexity is so great that it is bewildering to many, particularly to those who have not followed the most recent methods of dealing with the vegetation and gross physical environment. For convenience in handling, this complex may be broken up advantageously into smaller systems or units which are the agencies which influence animals. This plan provides for both their qualitative and quantitative relations, because the agents provide for the qualitative units, and their dynamic relations include their quantitative intensities.

In dealing with the interaction of systems relating to animals, one of the first points to consider is the classification of these systems, and the recognition of the sizes of the units. Many groupings are possible, such as the individual animal, its plant and animal associates, and the numerous factors of the physical environment. Further analytical systems of the vegetational environment can be grouped according to the recognized units current among the students of the genetic aspects of vegetational development (see Cowles, Clements, etc.). For the physical environment the geologists, physiographers and geographers have already made much progress in the analysis of unit systems, which can be used with comparative ease (see Chamberlin, Salisbury, Van Hise, Davis ('09), etc.). In the study of all these systems naturally more progress has been made in their recognition, than in their complex modes of interaction; and the formulation of their laws of interaction is of the greatest importance. There are three models which really come to mind in this connection. These are:

1. The physical model of the interaction of forces, which leads to resultant motion.

2. The application of Bancroft's law to the interaction of all systems.

3. The application of the physical and chemical model of the phase rule of Gibbs to equilibria of all kinds.

These will now be considered in their respective order:

1. The physical model will assist in keeping in mind

the underlying relations that the stresses, exerted by agents, will reinforce, overcome or balance one another, and influence the end result of change. This is a quantitative law. The *inertia* of the process of adjustment, and the *inertia* of equilibria, should be recalled (cf. Newton's first law) in this connection. The conception of inertia appears to have been almost neglected in biology.

2. Bancroft's law, that systems tend to change to minimize external disturbance, is a general law which appears to apply to the *interaction of all systems*. This is a qualitative law, which should be of great practical value.

3. The phase rule, according to Henderson ('13, pp. 257–258) is that the

condition of equilibrium in any material system depends upon the number of its components, the number of its phases, temperature, pressure, and in general, the concentrations of all the components . . . [as to] the term "component" and "phase" it will here suffice to say that in general the number of components increases as the number of separate chemical individuals increases, and that a phase is any solid, liquid or gaseous part of the whole system which possesses homogeneity of composition. For instance, if a system is made up of sand, salt solution, ice and aqueous vapor, each of these separate parts in that it is homogenous, is a phase. . . . Other things being equal, the greater number of phases, the less the tendency to change.

The quantitative character of this rule makes its application one of great difficulty, but it will serve as a guide or model for the organization of problems, and suggests the form into which experimental data should be organized, and secured for testing its application and validity.

The following extracts from Findlay ('04, pp. 8–18) will assist in gaining some of the general ideas involved in this subject:

A heterogenous system is made up of different portions, each in itself homogeneous, but marked off in space and separated from the other portions by bounding surfaces. These homogeneous, physically distinct and mechanically separable portions are called *phases*. Thus ice, water, and vapor, are three phases of the same chemical substance—water. A phase, however, whilst it must be physically and chemically homogeneous, need not necessarily be chemically simple. . . . The *number of phases* which can exist side by side may vary greatly in different systems. In

all cases, however, there can be but one gas or vapor phase on account of the fact that all gases are miscible with one another in all proportions. In the case of liquid and solid phases the number is indefinite, since the above property does not apply to them. . . . It is important to bear in mind that equilibrium is *independent of the amounts* of the phases present.

By component (p. 10) is

meant only those constituents, the concentration of which can undergo *independent* variation in the different phases, and it is only with these that we are concerned here. . . . The Phase Rule is concerned merely with those constituents which take part in the state of real equilibrium; for it is only to the final state, not to the processes by which that state is reached, that the Phase Rule applies. (Pp. 11–13.) It is, however, only in the case of systems of more than one component that any difficulty will be found; for only in this case will a choice of components be possible. . . . Now, although these constituents take part in the equilibrium, they are not all to be regarded as components, for they are not mutually independent. . . . In deciding the number of components in any given system, not only must the constituents chosen be capable of independent variation, but a further restriction is imposed, and we obtain the following rule: *As the components of a system there are to be chosen the* SMALLEST NUMBER *of independently variable constituents by means of which the composition of each phase participating in the state of equilibrium can be expressed in the form of a chemical equation.* . . . Another method may be given by which the number of components present in a system can be determined. Suppose a system consisting of several phases in equilibrium, and the composition of each phase determined by analysis. If each phase present, regarded as a whole, has the same composition, the system contains only one component, or is of the first order. If two phases must be mixed in suitable quantities in order that the composition of a third phase may be obtained, the system is one of two components or of the second order; and if three phases are necessary to give the composition of a fourth coexisting phase, the system is one of three components, or of the third order. . . . Again, therefore, we see that, although the number of the components of a system is definite, a certain amount of liberty is allowed in the choice of the substances; and we also see that the choice will be influenced by the conditions of experiment.

Summing up, now, we may say:

1. The components are to be chosen from among the constituents which are present when the system is in a state of true equilibrium, and which take part in that equilibrium.

2. As components are to be chosen the *smallest number* of such constituents necessary to express the composition of each phase partici-

pating in the equilibrium, zero and negative quantities of the components being permissible.

3. In any given system the *number* of the components is definite, but may alter with alteration of the conditions of experiment. A certain freedom of choice, however, is allowed in the (qualitative, not quantitative) selection of the components, the choice being influenced by considerations of simplicity, suitability or generality of application.

We see, therefore, that in case of some systems two, in other cases, only one of the independent variables (temperature, pressure, concentration) can be altered without destroying the nature of the system; while in other systems, again, these variables have all fixed and definite values. We shall therefore define the number of degrees of freedom of a system as the *number of the variable factors, temperature, pressure, and concentration of the components, which must be arbitrarily fixed in order that the condition of the system may be perfectly defined.*

A knowledge of its variability is, therefore, of essential importance in studying the condition and behavior of a system, and it is the great merit of the Phase Rule that *the state of a system is defined entirely by the relation existing between the number of components and the phases present,* no account being taken of the molecular complexity of the participating substances, nor any assumption made with regard to the constitution of matter. It is, further, as we see, quite immaterial whether we are dealing with "physical" or "chemical" equilibrium; in principle, indeed, no distinction need be drawn between the two classes, although it is nevertheless often convenient to make use of the terms, in spite of a certain amount of indefiniteness which attaches to them—an indefiniteness, indeed, which attaches equally to the terms "physical" and "chemical" process.

The Phase Rule of Gibbs, now, which defines the condition of equilibrium by the relation between the number of coexisting phases and the components, may be stated as follows: A system consisting of n components can exist in $n+2$ phases only when the temperature, pressure, and concentration have fixed and definite values; if there are n components in $n+1$ phases, equilibrium can exist while one of the factors varies, and if there are only n phases, two of the varying factors may be arbitrarily fixed. This rule, the application of which, it is hoped, will become clear in the sequel, may be very concisely and conveniently summarized in the form of the equation—

$$P+F=C+2, \text{ or } F=C+2-P$$

where P denotes the number of the phases, F the degrees of freedom, and C the number of components. From the second form of the equation it can be readily seen that the greater the number of the phases, the fewer are the degrees of freedom. With increase in the number of phases, therefore, the condition of the system becomes more and more defined, or less and less variable. . . .

Systems which are apparently quite different in character may behave in a very similar manner. Thus it was stated that the laws which govern the equilibrium between water and its vapor are quite analogous to those which are obeyed by the dissociation of calcium carbonate into carbon dioxide and calcium oxide; in each case a certain temperature is associated with a definite pressure, no matter what the relative or absolute amounts of the respective substances are. And other examples were given of systems which were apparently similar in character, but which nevertheless behaved in a different manner. The relations between the various systems, however, became perfectly clear and intelligible in the light of the Phase Rule. In the case first mentioned, that of water in equilibrium with its vapor, we have one component—water—present in two phases, *i. e.*, in two physically distinct forms, viz., liquid and vapor. According to the Phase Rule, therefore, since $C=1$, and $P=2$, the degree of freedom F is equal to $1+2-2=1$; the system possesses one degree of freedom, as has already been stated. But in the case of the second system mentioned above there are two components, viz., calcium oxide and carbon dioxide, and three phases, viz., two solid phases, CaO and $CaCO_3$, and the gaseous phase, CO_2. The number of degrees of freedom of the system, therefore, is $2+2-3=1$; this system, therefore, also possesses one degree of freedom. We can now understand why these two systems behave in a similar manner; both are univariant, or possess only one degree of freedom. We shall therefore expect a similar behavior in the case of all univariant systems, no matter how dissimilar the systems may otherwise appear. Similarly, all bivariant systems will exhibit analogous behavior; and generally, systems possessing the same degree of freedom will show a like behavior. In accordance with the Phase Rule, therefore, we may classify the different systems which may be found into invariant, univariant, bivariant, multivariant, according to the relation which obtains between the number of the components and the number of the coexisting phases; and we shall expect that in each case the members of any particular group will exhibit a uniform behavior. By this means we are enabled to obtain an insight into the general behavior of any system, so soon as we have determined the number of the components and the number of the coexisting phases.

In the preceding quotations there are certain points to which special attention should be called:

1. The phase rule is concerned with equilibria, and not with the processes by which this state is reached. It thus supplements Bancroft's law in a very important manner, because that law is mainly concerned with the process of developing equilibria. To make complete continuity and

contact between these two methods and to fuse them into *one cycle* Bancroft's should also be quantitatively expressed (the interacting systems). The importance of this is evident. I have not seen attention called to this fact, or the intimate relation between these two laws.

2. The number of components, phases, independent variables, concentrations, etc., to which the phase rule applies, is also one of the most marked features of biological problems in its dealing with the relation of animals to diverse environmental conditions and media.

3. The analysis of biological problems into cycles of action, systems, and agencies, is a necessary simplification of the biological problems, and is preliminary to the determination of the number of components, phases, and concentrations which are involved in the application of the phase rule to equilibria, and to Bancroft's law of their development. Even in case of biological problems which have not been reduced to quantity this model of dynamic relations should be of much assistance in clarifying working plans, especially in associational studies.

4. Improvements in the dynamic theory will probably simplify its application to biology. The detailed non-mathematical expression of these correlations will facilitate their wider use in biology, and it is also equally evident that with an adequate mathematical equipment the biologist's application of these ideas would be greatly facilitated.

The phase rule has been so valuable chemically that a special effort should be made to use it as much as possible as a model in biological work. Mellor ('04, pp. 183–184) says: "Gibbs' phase rule is the best system extant for the classification of equilibria—chemical and physical. All changes, both physical changes of state and changes of chemical composition, are found to depend upon the same general laws." Henderson ('13, p. 260) remarks: "There can be no doubt that, when feasible, the ideal method—from the physico-chemical point of view—to de-

scribe a material system is in terms of the phase rule.''[8]

To apply these principles to the interaction of systems is the great practical problem. It requires, as previously mentioned, the analysis of the problem to such a degree as to distinguish its different systems and homogeneous units, their degrees of freedom, their directions of change, their cycles, their dynamic status and their quantitative relations. Many of these action systems have long been clearly recognized by plant and animal physiologists and ecologists, as cells, tissues, organs and communities, and many are recognized also in the physical and chemical world, where much attention is given to dynamic relations.

The processes of integration and dominance tend to limit this diversity of systems. It is believed, however, that to strive consciously for the application of these conceptions with some idea of what they imply, will, however, greatly hasten progress. Further, by calling attention to these general ideas it may enable some investigators to become better prepared for handling them, because we may well recall Pasteur's remark that: ''In the fields of observation chance favors only the mind which is prepared.'' It is hoped that by emphasizing these relations others better qualified than I am will give attention to this subject, and supply numerous examples in the various specialties; for it is by this method largely that others can become interested and extend the applications.

Up to this point the discussion has been mainly devoted to the development of a dynamic conception of systems and their methods of interaction. The migration of animals has long been recognized to include not only those caused by the activities of the animal itself, but also by the activity or agency of their environment; it is there-

[8] Henderson ('13) does not mention Bancroft's law or attempt to relate it to the phase rule. In my ''Guide'' ('13, p. 85) special attention was called to both Bancroft's law and the phase rule by listing these first among papers on dynamics. Recently, since this paper was written, I have seen Henderson's ('17, p. 138) criticism of Spencer's ''stability of the homogeneous,'' to which he applies the phase rule and refers also to Bancroft's law, although not as here advocated.

fore now necessary to review briefly some of the main environmental agencies and processes operative. The geologists and physiographers have made much progress in the dynamic interpretation of their problems, so that it is a relatively simple matter to adapt their results to our purpose. They have shown that the rocks below the ocean are heavier than those of the land and that the present shores of the oceans change as a dynamic equilibrium is established between the heavier sea bottom and the lighter land area (Willis, '11). We have in this a cause for innumerable changes in the physical features of the earth's surface, and in the environments of animals. This beautifully illustrates the fundamental unity and method of interaction between the liquid sea and the solid land systems. This is one of the huge physical cycles which illustrate every dynamic phase, from a condition of stress through the slow process of adjustment to strain —retarded by the rigidity of the earth's crust—on to a dynamic equilibrium. All the land area which remains above sea level is exposed to waves, the disintegrating influences of the atmosphere, and the erosion by wind and running water, all of which tend to cut down all land to sea level, and to deposit the heavy débris on the sea bottom, thus cumulatively destroying its relative equilibrium, and, supplemented by radio-activity, there are instituted cycles of stress, in an unending series.

In the equilibria existing between the land and the sea, the isotatic cycle, and the cycle of erosion or base-leveling, are found two phases of the most important gross influences in the physical causes of animal migration (cf. Woodworth, '94; Adams, '01). To this must be specifically included climatic cycles (Huntington, '14, and others) whose influence upon animal migration is also profound. Intimately related to the preceding physical factors are the cyclic changes in the vegetational covering of the earth, particularly those recognized in recent years by the plant ecologists (Cowles, '11; Clements, '16, and others). The physical changes influence all organisms,

and operate in both short and long cycles, the various cycles traveling at diverse rates and mutually influencing one another in their adjustments to pressure. In these wonderful moving systems of cycles can be visualized the essence of modern scientific conceptions. From electrons, atoms, molecules, chemical compounds, colloids, cells, tissues, organs, individuals, and culminating in the community and association, is seen in each a dynamic center or microcosm, about which revolves other systems, in turn revolving as a part of a larger system in ever widening expansion, each in turn subordinated to a higher order of dominance, the culmination of interacting systems.

I have now completed an outline of the fundamental dynamic principles which are necessary as a background for my discussion of animal migration. These general principles appear to underlie all processes of animal regulation internal and external, and are expressions of these laws of interacting systems.[9]

[9] Although the preceding discussion is intended to bear mainly on migration, it should not be inferred that I would limit it in this manner. It is my belief that these general principles are of relatively wide application.

(*To be continued*)